The Biomechanics of Underwater Walking in Animals and Biomimetic Robots

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The colonization of land by aquatic animals is one of the greatest evolutionary transitions in the history of life on Earth. This dramatic evolutionary transition simultaneously provided the opportunity to diversify into a wide range of unoccupied niches while also posing significant challenges to almost every aspect of their physiology, ecology, life history, and biomechanics. But long before they ventured onto land, these ancient animals took their first steps underwater as they moved along the bottoms of rivers, lakes and oceans. This uniquely substrate-based mode of aquatic locomotion, termed henceforth "underwater walking", has received only scant study in spite of its evolutionary importance and potential for inspiring biomimetic robotics.

Underwater walking occurs in every group of aquatic animals with legs, from some of the earliest multicellular life to modern species. These species differ in buoyancy and regulation thereof, skeleton type and material, overall size, appendage type, and even number of legs and overall symmetry (radial vs bilateral). Several of these animals are secondarily aquatic and amphibious (e.g. crocodiles, turtles, hippopotami), while others walk along the bottom without ever having made the transition to land (e.g. benthic sharks, many crabs). The number and taxonomic breadth of convergences upon underwater walking suggests that it offers significant benefits, including ones which could be applied to biomimetic robots using this locomotor strategy, such as energetics, control, and the ability to traverse cluttered aquatic environments.

The potential energetic advantages of underwater walking are significant, including both increased in propulsive economy and reduced losses. Underwater walkers have the advantage of being able to generate propulsive reaction forces against an (ideally) rigid substrate, with neither the losses inherent in imparting momentum to flows nor the strong dependence upon speed; the reduced need to generate force to support the body weight will further allow the underwater walker to focus muscular effort on propulsive force generation. During station-keeping, underwater walkers can simply anchor themselves to the substrate using energetically efficient or even passive mechanisms, consuming minimal energy, in contrast to pelagic swimmers which must generate constant hydrodynamic forces to maintain orientation and to counteract any flow.

Cluttered environments, however, are where underwater walkers truly shine; objects which pelagic swimmers must avoid, underwater walkers may use as additional points of force generation. Indeed, the need to move through dense, swampy vegetation may have driven the evolution of legs in early tetrapods, and may be particularly conducive to effective locomotor force generation. Cluttered environments offer a range of surface orientations for the animal's limbs to interact with, allowing them to generate primarily propulsive forces without the risk of slipping, and the benefits of engaging which these substrates may have led to the evolution of digits, as seen in tetrapods. Additionally, the surrounding water will provide a natural damper against perturbations and eliminate the danger of collisions and falling, minimizing the need for both body support and rapid stabilizing feedback. Consequently, underwater walkers may be

able to easily traverse complex substrates without careful coordination or sophisticated feedback, like the feed-forward locomotion of small terrestrial runners with elastic limb structures, allowing robust control of biomimetic underwater walking robots.

This project seeks to examine the biomechanics of this under-studied mode of locomotion using novel tools and methods. To understand the dynamics of underwater walking in living animals, we must know the forces applied to the substrate, which in turn requires an

unconventional approach due to the small magnitude of the forces and underwater environment. To resolve this, we plan to use photoelastic polymer gels, materials which exhibit stress-dependent bifringence and consequently, when placed between two crossed light polarizers, will show flashes of light at the point of force application. These materials have seen sporadic use for measuring small locomotor forces, such as single-leg forces in running



Figure 1 – A tiger salamander walking terrestrially on photoelastic gel. The bright areas at the left forefoot and right hindfoot show force application.

cockroaches, but no systematic protocols or analysis methods have been developed in spite of their potential utility; as part of this project, we will develop protocols for material preparation and calibration, and publish open-source code for analysis of the resulting data. Using this technique, we will combine measurements of force, joint kinematics, and muscle activity under a variety of environments to gain a deeper understanding of the fundamental dynamics and neuromechanical control of underwater walking in morphologically diverse model species.

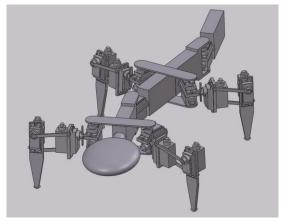


Figure 2 – A preliminary design of the underwater walking robot, using commercial waterproof servomotors and 3D printed parts. Hydrodynamic shell omitted for clarity.

Biomimetic underwater walking robots will also be central to this study, not simply as an endpoint to demonstrate the ability to replicate and understand the core concepts learned from biology, but as an experimental tool in and of themselves. Robots which can replicate the fundamental dynamics of animal locomotion can be used to explore the consequences of alternative morphologies, control strategies, behaviors, and environments, allowing the assessment of parameter combinations and possible behaviors which animals will not voluntarily engage in. This data allows for construction of a "mechanical fitness landscape", which can inform us whether the conditions seen in

animals are truly optimal and, if not, what mechanical or evolutionary tradeoffs the animals face.

This unique combination of comparative biomechanics and biomimetic robotics will allow a deeper understanding into the dynamics of underwater walking and how this form of locomotion can be used in biomimetic robotic vehicles in the future,